

Renaming the "Henneman Size Principle"

The principle that the orderly recruitment of motoneurons is based on variation in size, with the smaller neurons activated first, is credited to Harvard University physiologist Elwood Henneman, who first published a description of this theory in *Science* (Reports, 27 Dec. 1957, p. 1345). Having recently been asked to annotate an early basic science paper by the late eminent experimental neurologist Derek Denny-Brown, who was one of C. S. Sherrington's last students, we were surprised to find the "Henneman principle" clearly stated in a 1938 article Denny-Brown wrote with J. B. Pennybacker (1) which demonstrated that electromyography could be used to distinguish various involuntary muscle contractions such as fibrillations, fasciculations, and cramps in patients: "A particular voluntary movement appears to begin with discharge of the same motor unit. More intense contraction is secured by the addition of more and more units added in a particular sequence. This 'recruitment' of motor units into willed contraction is identical to that occurring in certain reflexes. The early motor units in normal gradual voluntary contraction are always in our experience small ones. The larger and more powerful units,

each controlling many more muscle fibers, enter contraction late" (1, p. 324).

The article by Denny-Brown and Pennybacker was not cited in Henneman's 1957 paper, nor in later works (2), although it clearly should have been. Apparently, Henneman was unaware of the Denny-Brown and Pennybacker paper, because he stated in 1968, "The enormous differences in cell size found in various types of neurons in the central nervous system intrigued early histologists and provoked many speculations, but the functional significance of cell size did not become apparent until recently," (3). This omission is particularly perplexing given the fact that Denny-Brown and Henneman were contemporaries at Harvard. Regardless, we suggest that if an eponym is to be associated with the "size principle," the correct association should be with Denny-Brown and Pennybacker.

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References and Notes

1. D. Denny-Brown and J. B. Pennybacker, *Brain* **61**, 311 (1938).
2. E. Henneman, G. Sonjen, D. Carpenter, *J. Neurophysiol.* **28**, 581 (1965).
3. E. Henneman, in *Medical Physiology*, V. Montcastle, Ed. (Mosby, St. Louis, MO, 1968), p. 1724.
4. We are grateful to D. Stuart and R. Enoka for discussion of this issue. Supported by PHS grant NS33782, which also supports our efforts at cataloging the Denny-Brown Research Collection [J. A. Vilensky, S. Gilman, E. Dec, *Ann. Neurol.* **60**, 247 (1994)].

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Populations as "Species-in-Waiting"?

Given the importance of populations in ecosystem function and stability, attempts to estimate the total number of populations on the planet are critical for science and public policy. However, the report "Population diversity: Its extent and extinction" (24 Oct., p. 689) by J. B. Hughes *et al.* has two problems.

First, the estimate of the number of populations per area of a sample of species should have used the arithmetic mean of populations per area, $\langle P \rangle$, not the geometric mean (1). Second, because the number of populations per species, Z , must be at least 1, P must

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